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Climate change shifts forward flowering and reduces crop waterlogging stress

Ke Liu^{1,2}, Matthew Tom Harrison^{2*}, Sotirios V. Archontoulis³, Neil Huth⁴, Rui Yang¹, De Li Liu⁵,
Haoliang Yan¹, Holger Meinke², Isaiah Huber³, Puyu Feng⁶, Ahmed Ibrahim², Yunbo Zhang^{1*},
Xiaohai Tian¹, Meixue Zhou²

¹Hubei Collaborative Innovation Center for Grain Industry/School of Agriculture, Yangtze University, Jingzhou 434025, Hubei, China

²Tasmanian Institute of Agriculture, University of Tasmania, Burnie 7320, Tasmania, Australia

³Department of Agronomy, Iowa State University, Ames, IA 50011, United States

⁴CSIRO, PO Box 102, Toowoomba 4350, Queensland, Australia

⁵New South Wales Department of Primary Industries, Wagga Wagga Agricultural Institute, Wagga Wagga, New South Wales, Australia

⁶College of Land Science and Technology, China Agricultural University, Beijing 100193, China

*Corresponding author:

yunbo1022@126.com (Prof. Yunbo Zhang);

matthew.harrison@utas.edu.au (Dr. Matthew Tom Harrison)

Abstract

Climate change will drive increased frequencies of extreme climatic events. Despite this, there is little scholarly information on the extent to which waterlogging caused by extreme rainfall events will impact on crop physiological behaviour. To improve the ability to reliably model crop growth and development under soil waterlogging stress, we advanced the process-basis of waterlogging in the farming systems model APSIM. Our new mathematical description of waterlogging adequately represented waterlogging stress effects on the development, biomass and grain yield of many commercial Australian barley genotypes. We then used the improved model to examine how optimal flowering periods (OFPs, the point at which long-term abiotic stresses are minimal) change under historical and future climates in waterlogging-prone environments, and found that climate change will reduce waterlogging stress and shift forward OFP (26 days earlier on average across locations). For the emissions scenario Representative Concentration Pathway (RCP) 8.5 at 2090, waterlogging stresses diminished but this was not enough to prevent substantial yield reduction

due to increasingly severe high temperature stress (–35% average reduction in yield across locations, genotypes and sowing dates). It was shown that seasonal waterlogging stress patterns under future conditions will be similar to those occurring historically. Yield reduction caused by waterlogging stress was 6% and 4% on average across sites under historical and future climates. To adapt, both genotypic and management adaptations will be required: earlier sowing and planting waterlogging tolerant genotypes mitigate yield penalty caused by waterlogging by up to 26% and 24% under historical and future climates. We conclude that even though the prevalence of waterlogging in future will diminish, climate change and extreme climatic events will have substantial and perverse effects on the productivity and sustainability of Australian farms.

Keywords: Breeding, climate change, extreme climatic events, environmental characterisation, tolerance

1. Introduction

Climate change predictions herald increased frequencies of extreme climatic events, with historical analysis by the IPCC indicating statistically significant increases in the number of high precipitation events (e.g. 95th percentile) in many regions (Seneviratne *et al* 2012). Increased frequencies of extreme rainfall events result in more flash flooding and seasonal waterlogging, though effects of superfluous water on crop growth and development have not been well studied (Chang-Fung-Martel *et al* 2017).

Waterlogging is highly variable and multifaceted, both temporally and spatially. Waterlogging may occur for many reasons, including geography, aspect, extreme rainfall events, high and prevalent seasonal rainfall, poor hydraulic conductivity, lateral groundwater flows, rising/perched water tables, improper irrigation management or combinations of these factors (Shaw *et al* 2013, Liu *et al* 2020b). In Australia, waterlogging primarily occurs in regions that have higher growing season rainfall, thin topsoils and/or low soil permeability. These factors prevent drainage and cause surface water accumulation. In both rainfed and irrigated environments,

waterlogging may occur at any stage of crop development. Grain yield penalties tend to be highest when waterlogging occurs around heading. Waterlogging at this critical stage can reduce grain yield by up to 70%, with losses primarily attributed to reduced spikelet fertility and grain weight (Liu *et al* 2020a, Ploschuk *et al* 2020, Setter and Waters 2003).

In Australia, the States of Western Australia and Victoria produce around 32% and 16% of the national harvest respectively; of which 1.8 Mha in Western Australia are periodically waterlogged and 4 Mha in Victoria are at high risk of yield losses due to waterlogging (Shaw *et al* 2013). Collectively, potential Australia crop production losses due to waterlogging are around AU\$300 million per annum (Manik *et al* 2019). The winter crops most impacted by waterlogging include wheat and barley, Australia’s most predominant winter grains. Despite this, most commercial Australian cereal genotypes are waterlogging intolerant (Liu *et al* 2020a). There is thus a clear need for the development of management practices coupled with greater genotypic tolerance to waterlogging to help alleviate yield losses caused by waterlogging. Here, we identify the impact of waterlogging on crop yields at several representative sites, then quantify the relative value of waterlogging tolerant genotypes at both optimal (and sub-optimal) sowing times.

In addition to effects on soil waterlogging, climate change has and will result in warmer days that accelerate crop development and bring forward flowering times (Bell *et al* 2013, Pembleton *et al* 2016). Crop yields tend to be highest when flowering occurs in a window that minimises exposure to frost, heat and drought stress during the critical period for yield determination that occurs prior to and during flowering (Flohr *et al* 2017, Lilley *et al* 2019, Liu *et al* 2019). An understanding of the duration of the optimal flowering period (OFP) and the timing in which it occurs over the long term across environments and genotypes may be used as a tactical lever to help lower the risk of abiotic stress (Harrison *et al* 2011a, 2011b). While previous work has focussed on OFP in water limited environments, our knowledge of how OFPs may be affected in environments that are prone to waterlogging is still in its infancy. To disentangle the effects of waterlogging *per se* from that of sowing time on yield, we first simulated a range of sowing dates at each site to identify the OFP, then second

examined the relative influence of waterlogging on yield at the OFP.

Because waterlogging is a function of many environmental and social factors, our ability to reliably quantify the impacts of waterlogging on crops often suffers from poor reproducibility in field environments. This can make it difficult to identify management, genotypes or general agronomic practices that consistently alleviate effects of waterlogging. Some of these issues can be dealt with and appropriately scaled using simulation approaches (Liu *et al* 2020b). Indeed, process-based crop simulation models are becoming increasingly valuable frameworks in climate change adaptation of agricultural systems (Alcock *et al* 2015, Harrison *et al* 2016b, 2016c, Ho *et al* 2014). Suitably designed models can also be used to assess the interplay between long-term waterlogging frequencies, increasing temperatures and optimal flowering times.

While contemporary farming system models are highly versatile, many models have not been designed to capture stress effects caused by superfluous moisture or extreme events (Harrison *et al* 2012a, 2012b, Phelan *et al* 2015) though there are a few notable and recent exceptions. Ebrahimi-Mollabashi *et al* (2019) improved the ability of the Agricultural Systems Production Systems sIMulator (APSIM) to model the effects of waterlogging on root depth in APSIM-Soybean. Pasley *et al* (2020) built on the work by Ebrahimi-Mollabashi *et al* (2019), improving the ability of APSIM-Soybean to model the effects of waterlogging on photosynthesis, phenology and nitrogen fixation. In support of the work by Pasley *et al* (2020), a recent review showed that APSIM was one of the most appropriate extant farming systems models for simulating waterlogging because this model is equipped with soil and water modules that can adequately simulate shallow water table dynamic and account for appropriate mechanisms (e.g. photosynthesis, nitrogen leaching and denitrification, and an aeration stress determined by the sensitivity of different growth stages; Liu *et al* 2020b). While the preceding work has clearly improved our understanding and ability to simulate soil waterlogging, little attention has been placed on cereal crops such as barley. This is important, because biological responses of legumes such as soybean under waterlogging will likely differ to those in barley.

Here, we conducted a genotype by environment by management analysis ($G \times E \times M$) to examine yield impositions caused by waterlogging, frost and heat in sites prone to waterlogging across Australia. Specifically, the objectives of this study were to (1) improve the capacity of APSIM-Barley to reliably model waterlogging effects on barley growth and development, (2) determine how climate change will influence OFPs when waterlogging stresses are accounted for, (3) examine how waterlogging frequencies and seasonal typologies influence yield under current and future climates.

2. Materials and methods

2.1 Experimental design

Biophysical data were obtained from controlled environmental facilities at Mt Pleasant Laboratories (41°28'S, 147°08'E), Launceston, Tasmania in 2019 and 2020; see Liu *et al* (2020a) for details. Briefly, experiments were conducted with six barley genotypes (Macquarie, Franklin, Planet, Westminster, a backcross line, Macquarie (T) and a double haploid line called TAMF169 (Table 1). These barley differ in waterlogging tolerance conferred through aerenchyma formation under waterlogged conditions (for further background of these genotypes, see Zhang *et al* (2015) and Zhang *et al* (2016).

Table 1. Barley differing in waterlogging tolerance used in this study. T refers to waterlogging tolerance.

Genotype	Pedigree	Waterlogging tolerance	Source
Macquarie	Alexis/Gairdner//Gairdner	Intolerant	Commercial variety released by the University of Tasmania
Macquarie(T)	Macquarie/TAM407227//Macquarie	Tolerant	A backcross lines with the background of Macquarie and the waterlogging tolerance QTL from a wild barley, by the University of Tasmania
Westminster	NSL97-5547/Barke	Intolerant	A commercial variety released by GrainSearch
Franklin	Shannon/Triumph	Intolerant	A commercial variety released by the University of Tasmania
Planet	Tamtam/Concerto	Intolerant	A commercial variety released by Seed Force Pty Ltd

TamF169	TAM407227/Franklin	Tolerant	A doubled haploid line from the cross between TAM407227 and Franklin, by the University of Tasmania
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Four waterlogging treatments of varying duration and timing with respect to phenology were implemented: waterlogging at Zadok stage (ZS)12.5 for one or two months (WL1 and WL2, respectively), waterlogging at ZS15 for two months (WL3), and waterlogging beginning one day before heading for 15 days (WL4). Soil moisture of the controls were maintained at field capacity until grain filling. For treatment plots, waterlogging was achieved by raising an external water reservoir above the soil surface such that the water level within the plot increased to 400 mm so the soil was completely saturated. Further details of methods used to obtain experimental data used for the modelling in the current paper are described in Liu *et al* (2020a).

Table 2. Parameterised APSIM genotypic coefficients. Abbreviations: tt_end_of_juvenile (*TEJ*, thermal time from sowing to end of juvenile stage), tt_start_grain_fill (*TSGF*, thermal time at the beginning of grain filling), photop_sens (*PPD*, photoperiod sensitivity), vern_sens (*VERN*, vernalisation sensitivity), grains_per_gram_stem (*GPGS*, the number of grain per gram of stem), potential_grain_filling_rate (*PGFR*, grain growth rate during grain-filling stage).

Genotypes	<i>TEJ</i> (°Cd)	<i>TSGF</i> (°Cd)	<i>PPD</i>	<i>VERN</i>	<i>GPGS</i> (g)	<i>PGFR</i> (g·grain ⁻¹ ·day ⁻¹)
Macquarie	873	410	0.5	1.0	27.5	0.0029
Macquarie (T)	870	428	0.5	1.0	27.5	0.0025
Planet	590	440	2.3	1.0	28.8	0.0030
TamF169	620	430	2.1	1.0	28.0	0.0027
Franklin	710	410	2.2	1.5	27.0	0.0026
Westminster	890	410	0.3	1.0	27.7	0.0030

2.2 Model parameterisation and validation

Experimental data described above were used to parameterise and validate APSIM version 7.9 (Holzworth *et al* 2014). Genotypic phenology was calibrated by adjusting parameters of existing genotypes in the APSIM Barley XML file, or by adjusting the base cultivar where the genotype being calibrated did not exist in the

default APSIM release. The APSIM-SWIM Module (Huth *et al* 2012) was first initialised using control plots without waterlogging, with the watertable height maintained at 200 mm until grain filling. Measured data for phenology, biomass, yield component and grain yield of the six genotypes in Table 1 were then used to parameterise APSIM following procedures described by Harrison *et al* (2019) and Liu *et al* (2019). Parameterised values are shown in Table 2. Bulk density (BD) and volumetric soil water content at air dry, lower limit (LL, i.e. 15 bar), drained upper limit (DUL or field capacity) and saturation (SAT) were measured in the laboratory.

2.3 Sites used for the factorial analysis

The majority of Australian grain cropping systems are located within a relatively narrow land area. The cropping zone is colloquially known as the Australian Wheatbelt, spanning from southern-Queensland, to New South Wales (NSW), Victoria, South Australia (SA) and Western Australia (WA). These regions experience temperate or Mediterranean climates with winter-dominant rainfall and hot, dry summers. Since the 1990s, the Wheatbelt has experienced increasing frequencies of heat waves and frost (CCIA 2021) in concert with declining rainfall during the critical winter cereal sowing periods. Here, we selected twelve sites across Australian Wheatbelt for factorial analysis.

Table 3. Locations used to conduct the G x E x M including details of soil depth (SP), soil hydraulic conductivity (Ks), annual mean watertable depth (AMWD; Fan *et al* 2013) and total growing season rainfall (TGSR).

Groups	Locations	Lat, Long	SP (m)	Ks (mm/day)	AMWD (mm)	TGSR (mm)
Group 1: Low Ks						
	Euroa, VIC	-36.75, 145.60	1.2	7.9	550	553
	Naracoorte, SA	-36.95, 140.73	1.5	5.2	652	498
	Hamilton, VIC	-37.82, 142.06	1.2	5.0	850	552
	Furner, SA	-37.40, 140.32	1.0	3.6	662	624
Group 2: High- AMWD						
	Carrick, TAS	-41.54, 146.99	1.5	5.5	504	578
	Lismore, VIC	-37.95, 143.34	1.2	6.7	582	494
	Wandering, WA	-32.67, 116.67	1.0	42.8	552	542
	Millicent, SA	-37.56, 140.35	1.0	22.3	596	669
Group 3:						

High
TGSR

Robe, SA	-37.16, 139.79	1.0	49.1	579	569
Frankland, WA	-34.44, 116.99	1.0	36.7	1115	690
Albany, WA	-34.94, 117.80	0.8	44.4	1150	861
Mt Barker, WA	-34.63, 117.64	1.5	47.9	1528	637

At each location (Table 3), sowing was simulated at five-day intervals from 1 April to 15 July for three genotypes (Macquarie, Macquarie (T) and Planet) differing in their phenology and waterlogging tolerance. Macquarie and Macquarie(T) were used to compare the relative impact of waterlogging stress through improved genetics (the latter being waterlogging tolerant). Macquarie and Planet were used to compare whether fast or slow developing genotypes would be more suitable to future climates. Waterlogging may occur for many reasons, including extreme rainfall events, intense rainfall in short periods, poor hydraulic conductivity, rising/perched water tables, or combinations of these factors. To examine the extent to which these factors influence waterlogging stress, we systematically categorised sites into three key groups (Table 3): low hydraulic conductivity, high watertable (ie. close to the soil surface) and high growing season rainfall (Viscarra *et al* 2014). To ensure crops were successfully established at sowing, initial plant available water was set to zero and 15 mm of irrigation was added so that initial soil water content was standardised across simulations. All simulations using historical climate data assumed a baseline atmospheric CO₂ concentration of 380 ppm.

2.4 Climate scenarios

Historical daily climate data for maximum and minimum temperature, rainfall and solar radiation for the period of 1900-2019 were obtained as SILO point data (Jeffrey *et al* 2001) for each location. We developed future climate scenarios for the period of 2030 to 2149 (hereafter referred to as future climate scenarios with a median time horizon of 2090) using Representative Concentration Pathways (RCP) 8.5 (IPCC 2014, Schwalm *et al* 2020), representing a radiative forcing of 8.5 W m⁻² by the end of the century, because this scenario most closely matches the change in climate that has already be realised in Australia (Bell *et al* 2013; Chang-Fung-Martel *et al* 2017; Phelan *et al* 2015) and the world more generally (Schwalm *et al* 2020). Historical climate data

were used to produce future climate data for each region, in all cases with an atmospheric CO₂ concentration of 850 ppm following Collier *et al* (2011). The approach we used to produce future climate contained both monthly average trends in gradual climate change but also increased magnitudes and frequencies of extreme climatic events based on forecasts from regional climate models, such that climate data were more variable compared with historical climate observations. For each site, we used the historical climates as a template for modification, and all modifications were made on a daily time-step (see more details in Harrison *et al* 2016a). In this case, future climate dataset would have the same length as historical climate dataset. Averaged across locations, mean daily minimum and maximum temperature had increased by 1.6°C and 3.8°C respectively by 2150, while future average rainfall decreased by -35% relative to historical period (Fig. S1).

2.5 Optimal flowering and sowing windows

To examine how OFPs were influenced by waterlogging stress around flowering, we run a default version of APSIM simulation that included and not included waterlogging functions. OFPs were calculated for each genotype using a range of sowing dates (See methods described by Liu *et al* (2019)). Frost, heat and waterlogging-limiting yield (hereafter, ‘FHW’) for each year were calculated as the product of potential yield, cumulative frost and heat stress, and waterlogging stress. The OFP for a given location was identified as the flowering dates corresponding to ≥ 95% of the maximum 15-day running mean FHW.

2.6 Improving biological processes influenced by waterlogging in APSIM-Barley

In the APSIM source code via the executable, we implemented the waterlogging processes documented by Ebrahimi-Mollabashi *et al* (2019) and Pasley *et al* (2020). Effects of waterlogging on photosynthesis and phenology in the APSIM source code were represented by the new functions *oxdef_photo* and *oxdef_pheno*, respectively. Each waterlogging function assumes 0–1 multipliers in the form of “x/y pairs” (Holzworth and Huth, 2009), where x is the independent variable (e.g. soil moisture) and y is the response variable (e.g. photosynthesis and phenology), wherein x = 0 when the soil is at field capacity (no stress) and x = 1 when the soil is saturated (full

stress). These functions were invoked when 80% of the roots become waterlogged (Fig. 1a).

Our previous studies have shown that waterlogging affects both photosynthesis and phenology to varying degrees depending on the timing and duration of waterlogging. We thus modelled the impacts of waterlogging as a function of crop stage (*oxdef_photo*, Fig. 1b), which is a significant advance on the majority of previous studies that assume that waterlogging stress depends only on water-filled pore space. Similarly, our experimental work has shown that waterlogging delays crop development, and in some cases induces premature senescence (Liu *et al* 2020a). The phenology function we added to APSIM (*oxdef_pheno*) was derived using information from environment-controlled experiments (Liu *et al* 2020a; Pasley *et al* 2020). We first initialised APSIM for the (non-waterlogged) control using APSIM's SWIM3 Module, then later tested the new functions using data measured in the waterlogging treatments. Parameterised values are shown in Fig. 3b.

To examine the extent to which the new processes added to APSIM-Barley improved the ability to simulate crop growth and development under waterlogging, we also run a default (unimproved) version of APSIM-Barley with waterlogging. Simultaneous multi-objective optimisation (Harrison *et al* 2019) of *oxdef_photo* and *oxdef_pheno* for each of the six genotypes (Table 2) was performed using the 2019 dataset for the four waterlogging treatments by minimising the sum of squared residuals across datasets.

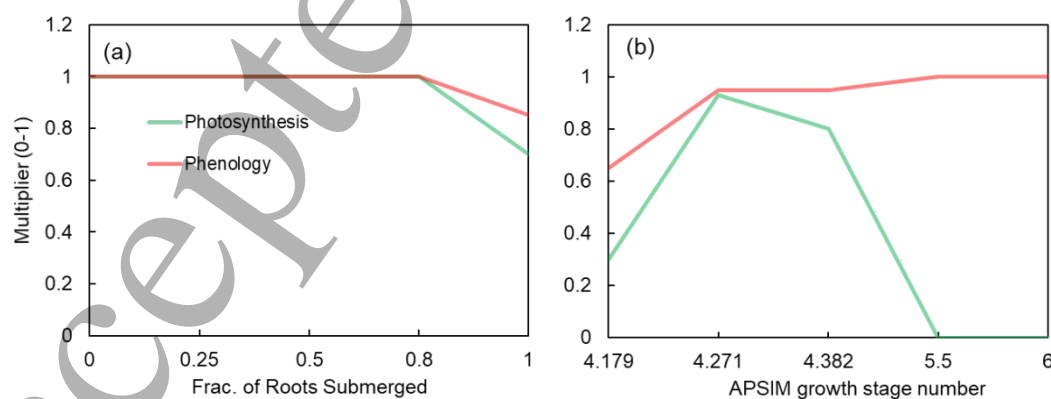


Fig. 1. Waterlogging stress factors for photosynthesis and phenology derived and parameterised in this study. Effects of waterlogging on root growth (lower panel) are part of the default APSIM 7.9 release but are shown here for completeness.

2.7 Long-term seasonal waterlogging-stress typologies and frequencies

To characterise common waterlogging stress typologies, we output seasonal time courses of photosynthetic stress relative to phenology (i.e. *oxdef_photo*) and clustered these stresses across simulation years, sites, genotypes and management following the approach outlined by Harrison *et al* (2014). For each environment, *oxdef_photo* was averaged over 100°Cd increments from emergence to 450°Cd after flowering. We then characterised predominant seasonal water stress trends by applying *k*-means clustering to all seasonal trajectories of *oxdef_photo* against phenology. Clustering was applied using R statistical package (R Development Core Team, 2013), with clusters being defined such that total within-cluster variation was minimised (further details of this method are described by Chenu *et al* (2013).

3 Results

3.1 Performance of the default version of APSIM when crops were subjected to waterlogging

Without the waterlogging algorithms, the default version of APSIM Barley performed poorly in simulating waterlogging effects on grain yield, grain number maturity biomass and phenology (Fig. 2). Grain yield, grain number and maturity biomass were over-estimated across waterlogging treatments. Values of variation ratio (VR) ranged from 1.39 to 2.68. Flowering and maturity date were also over-simulated, with root mean square error (RMSE) ranged from 10.7 d in simulated anthesis to 5.6 d in simulated maturity.

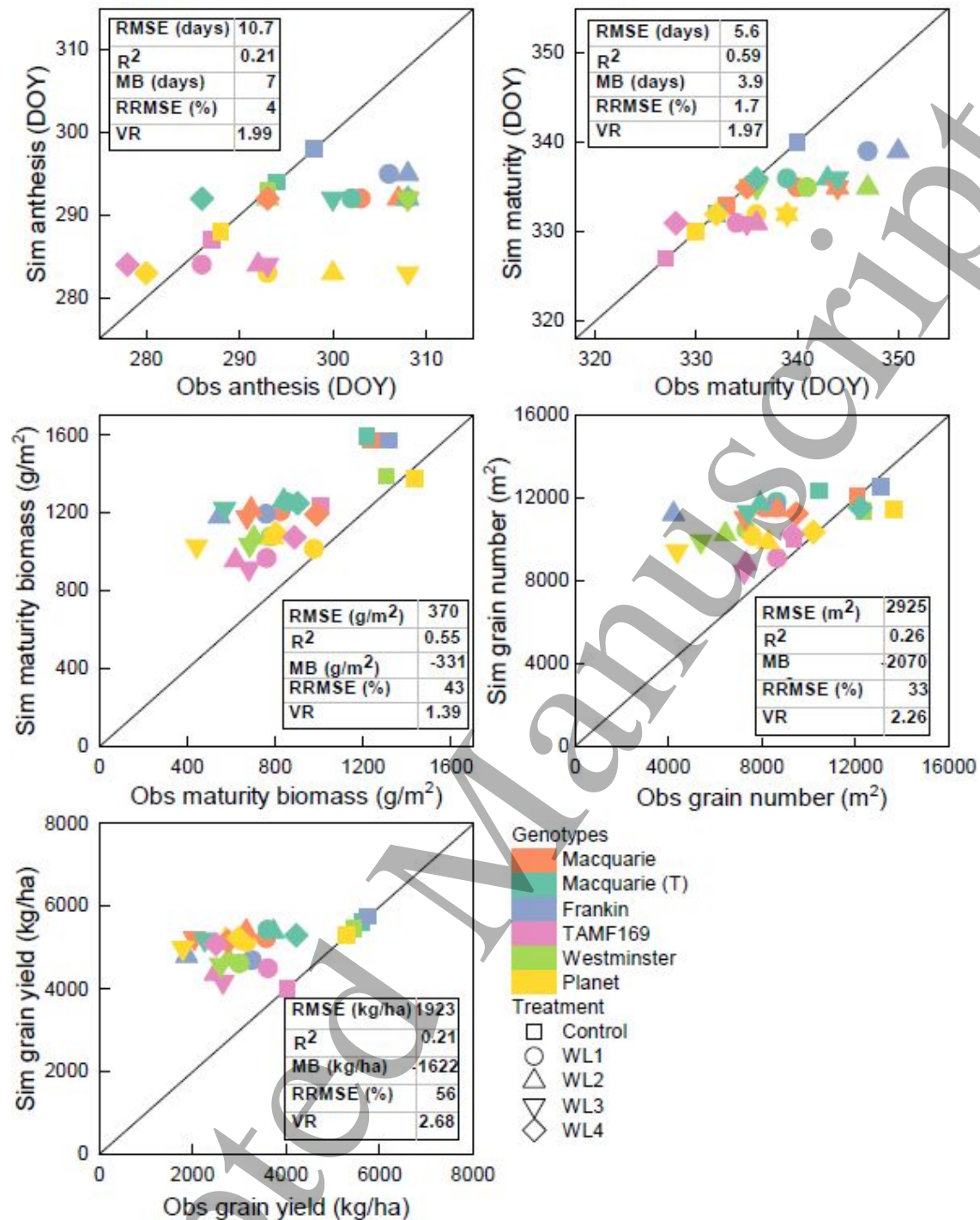


Fig. 2 Simulated and observed anthesis, maturity, grain number, maturity biomass and yield for the default version of APSIM without the effects of waterlogging on photosynthesis and phenology. Ideal simulations fall on the 1:1 line. WL1: waterlogging exposed at ZS12.5 for 1 month; WL2: waterlogging exposed at ZS12.5 for 2 months; WL3: waterlogging exposed at ZS15 for 2 months; WL4: waterlogging exposed at ZS59 for 15 days. The WL4 treatment was not conducted on Franklin and Westminster.

3.2 APSIM performance when the algorithms for modelling waterlogging are improved

Including the effects of waterlogging on photosynthesis and phenology significantly improved the ability of the model to simulate waterlogging (Fig. S3 &3). RMSE ranged from 4.9 d in simulated anthesis to 3.3 d in simulated maturity. Mean bias (MB) ranged from 1 d in simulated anthesis to -2 d in simulated maturity. Values of RMSE normalised by the mean of the observed data (RRSME) were low and R^2 values were greater than 0.70. Overall agreement between the simulated and observed maturity biomass, grain number and grain yield for all genotypes across treatments was within the variability implicit to the measured data, indicating adequacy of the parameterisation (Fig. 3). The model appropriately captured delays in phenology and thus reduced biomass accumulation during waterlogging periods, as well as the final yield and biomass response to waterlogging stress at different growth stages. An example of model validation that includes the simulated control and waterlogging treatments is shown in Fig. S3.

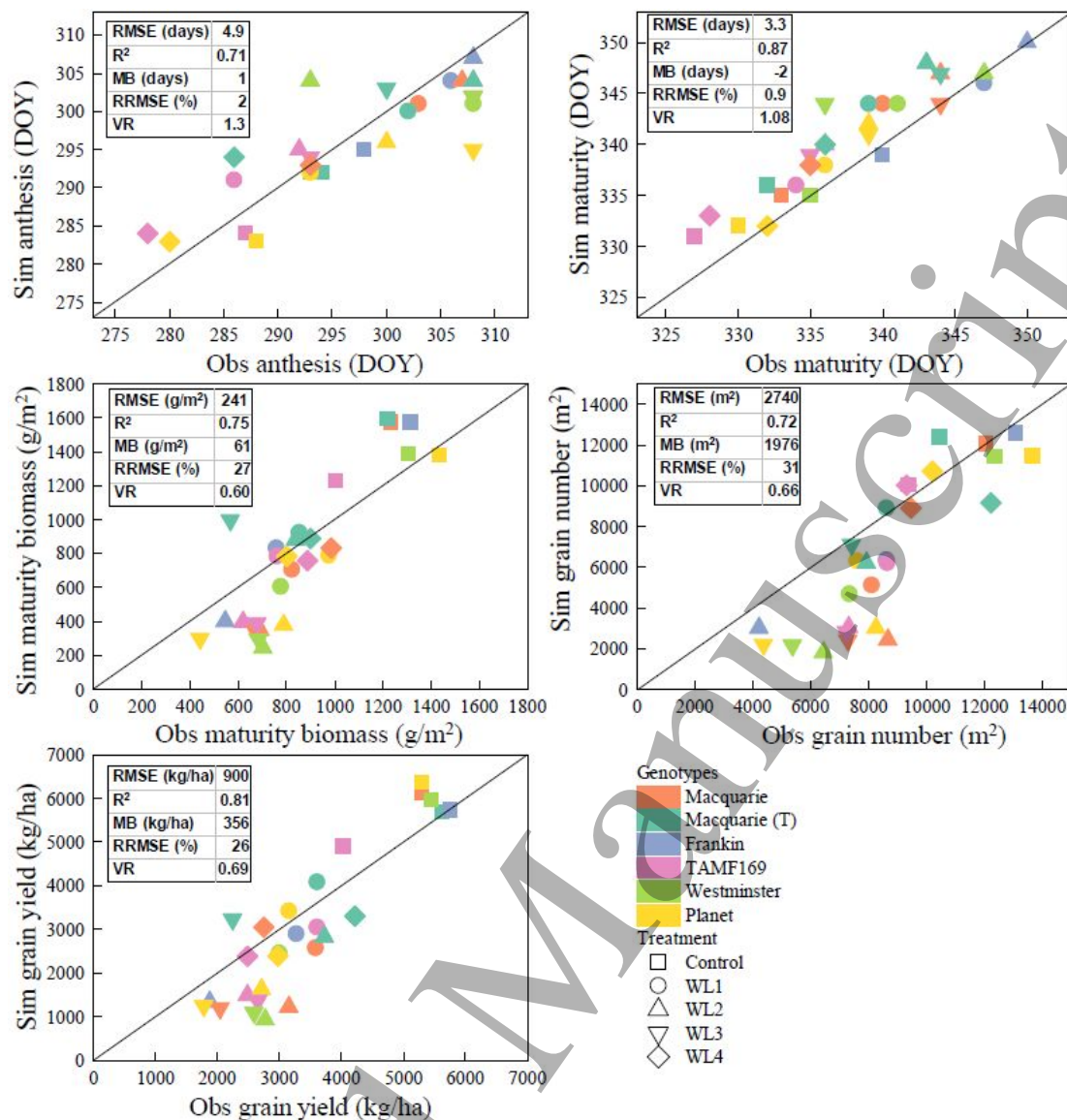


Fig. 3 Simulated and observed anthesis, maturity, grain number, maturity biomass and yield when the effects of waterlogging stress on phenology and photosynthesis are accounted for (*cf.* Fig. 6). Ideal simulations fall on the 1:1 line. Colours and shapes represent alternative genotypes and waterlogging treatments. WL1: waterlogging exposed at ZS12.5 for 1 month; WL2: waterlogging exposed at ZS12.5 for 2 months; WL3: waterlogging exposed at ZS15 for 2 months; WL4: waterlogging exposed at ZS59 for 15 days. The WL4 treatment was not conducted on Franklin and Westminster.

3.3 Optimal flowering periods under historical climates

Barley yields varied from 6,977 to 11,943 kg/ha across locations due to differences in environmental conditions (Fig. 4 and Tables S1). In most sites, mean peak yield increased from 1900 to 1939 before declining. Genotypes Planet and Macquarie had the highest peak mean yield at the site of Carrick in Tasmania, with an

average of 11,319 kg/ha due to a high growing season rainfall and cool temperature climate. The lowest peak mean yield was at Mt Barker in Western Australia with an average yield of 7,911 kg ha⁻¹ because of hot temperature. In general, OFP windows varied from September to November across sites and genotypes. Mt Barker (WA) had earliest OFP (9-Sep) whereas Carrick had the latest OFP (14-Nov). OFPs moved forward least at Albany (6 days) and the most (33 days) at Naracoorte. For most sites, warming climates have moved forwards OFPs due to increasing temperature and decreasing seasonal rainfall (Fig. S1).

3.4 Optimal flowering periods under future climates

In general, future climates reduced grain yield and moved forwards OFPs (Fig. 4 & Table S1). The sites of Hamilton and Tatyoon in Victoria experienced the largest yield loss (both approx. 56%), while Carrick in Tasmania experienced the lowest yield losses (16%). Generally, the start and end of the OFP at each site shifted forwards similarly across locations and genotypes. The start and close of the OFPs were 26 days earlier on average across locations. The largest shift was at Hamilton, Euroa and Lismore in Victoria because these sites had the greatest increases in maximum and minimum temperature (Fig. S1).

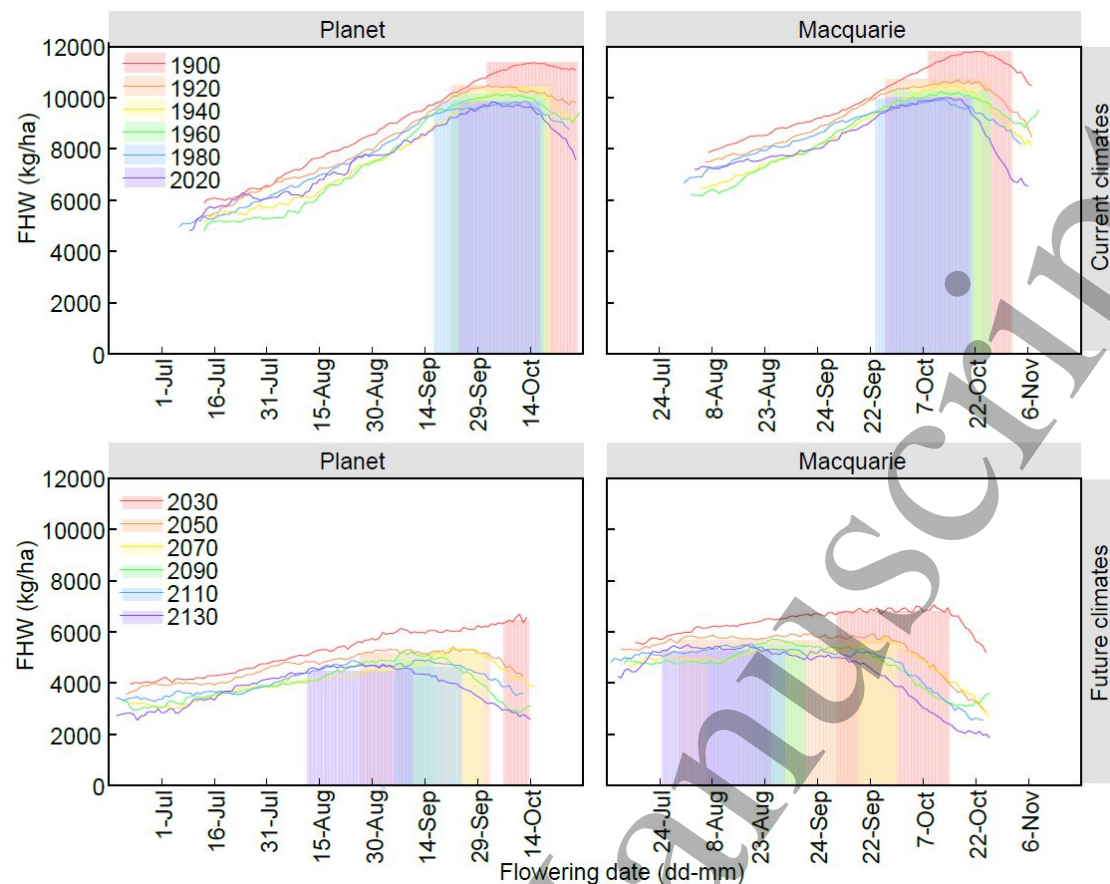


Fig. 4 Optimal flowering periods (shaded zones) under current and future climates for a short-season barley genotype Planet and a long-season genotype Macquarie at Wandering in Western Australia (for other sites, see Table S1). Lines represent the frost, heat and waterlogging limited 15-day running mean yield (FHW yield) and shaded zones represent the optimal flowering periods for 20 year increments from 1900 to 2130.

3.5 Relative importance of frost, heat and waterlogging stress in determining the OFPs

Sites with lower risk of aggregate stress during OFPs had higher mean yield (e.g. Carrick compared with short growing-season sites such Mt Barker in WA). Frost and waterlogging stress were the main stress affecting OFPs at Carrick in Tasmania and Euroa and Hamilton in Victoria.

Severe waterlogging stress can delay phenology, penalise grain yield and hence impact the timing of OFPs. We found that waterlogging occurred more frequently at sites with the combination of low soil hydraulic conductivity (Ks), high watertable and high growing season rainfall (e.g. Carrick and Furner). Our results suggest that

waterlogging stress needs to be considered when defining OFPs in waterlogging prone zones (Carrick, Funer and Hamilton, Fig. 5). OFPs were eight days earlier at Carrick in Tasmania and four days later at Tatyoon in Victoria if waterlogging effects were not considered. For other sites, waterlogging had a relatively minor effect on OFPs.

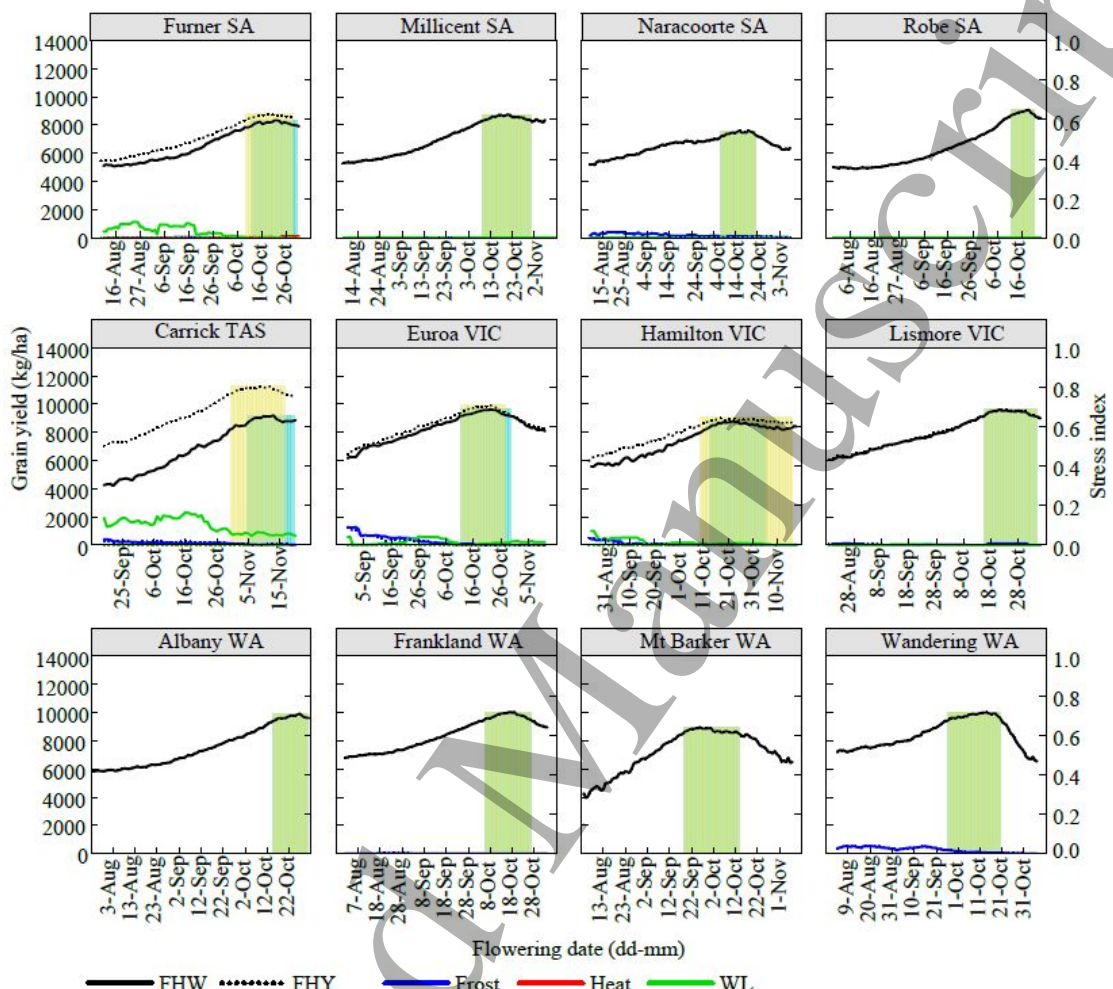


Fig. 5 Relationships between flowering and long-term average simulated frost, heat and waterlogged yield (FHY) for a mid-fast developing barley (Macquarie) under historical climates (2000-2019). Stress indices of frost (blue line) and waterlogging (green line), heat stress (red line) was low at these sites. Black dotted lines (FHY) represent yields limited by frost and heat stress, but not waterlogging stress. Black solid lines (FHW) represent yields limited by frost, heat stress and waterlogging stress. The optimal flowering period (shaded zones) is the flowering duration at which yield is greater than or equal to 95% of the long-term average peak yield (yellow regions exclude waterlogging functions; blue regions include waterlogging; green regions represent overlapping yellow and blue regions).

3.6 Waterlogging stress typologies and adapting to waterlogging stress through crop breeding and improved genetics

As most simulated sites suffered less waterlogging stress, here we only selected two representative sites with waterlogging risk to show waterlogging stress typologies in Fig. 6 (See other sites in Supplementary Figures). The three most prevalent waterlogging stress patterns accounted for 85% variation across all genotypes, sowing times, sites and climates (Fig. 6). Under historical conditions, Carrick and Hamilton experienced early-onset low waterlogging stress. In 2090, the two sites will have lower frequencies of waterlogging. Frequencies of waterlogging stress under future climates will shift away from early-onset medium waterlogging stress (EMS) and towards early-onset low waterlogging stress (ELS, increased by 5-23%) but overall stress typologies under future conditions were similar to those occurring at under present conditions.

Our previous work (Zhang *et al* 2015&2016) documents the development of new genotypes with waterlogging tolerance through aerenchyma formation. In the present study, we examined the performance of these new genotypes under conditions for which crops would be expected to experience waterlogging over the long-term. We showed that waterlogging-tolerant genotypes mitigated waterlogging-induced yield declines by 82-1,711 kg/ha across sites (Fig. 7). Benefits derived from the use of waterlogging tolerant genotypes were greatest at Carrick (Tasmania), followed by Hamilton (Victoria) and Furner (South Australia). Planting waterlogging tolerant genotypes (e.g. Macquarie (T)) prevented 819 to 2,800 kg/ha yield loss at Carrick in Tasmania, while the yield difference due to waterlogging tolerance was relatively minor (82-806 kg/ha) in Western Australia and South Australia under current climates.

Under future climates, waterlogging stress generally declined such that differences between waterlogging tolerant and susceptible genotypes diminished over time due to drying trends with climate change. However, some sites continue to experience significant waterlogging (e.g. Carrick), underscoring the need for the continued genetic development of waterlogging tolerant lines. The highest yield difference between the waterlogging tolerant and susceptible genotypes was 1,548 kg/ha at this site.

Yield reduction due to increasingly severe high temperature stress (~35% average reduction in yield across locations, genotypes and sowing dates) under the emissions scenario RCP8.5 at 2090 (Fig. 6). Euroa, Hamilton and Lismore in Victoria will suffer the most yield loss (*ca* 45% on average) and Carrick will suffer the least yield reduction (16%).

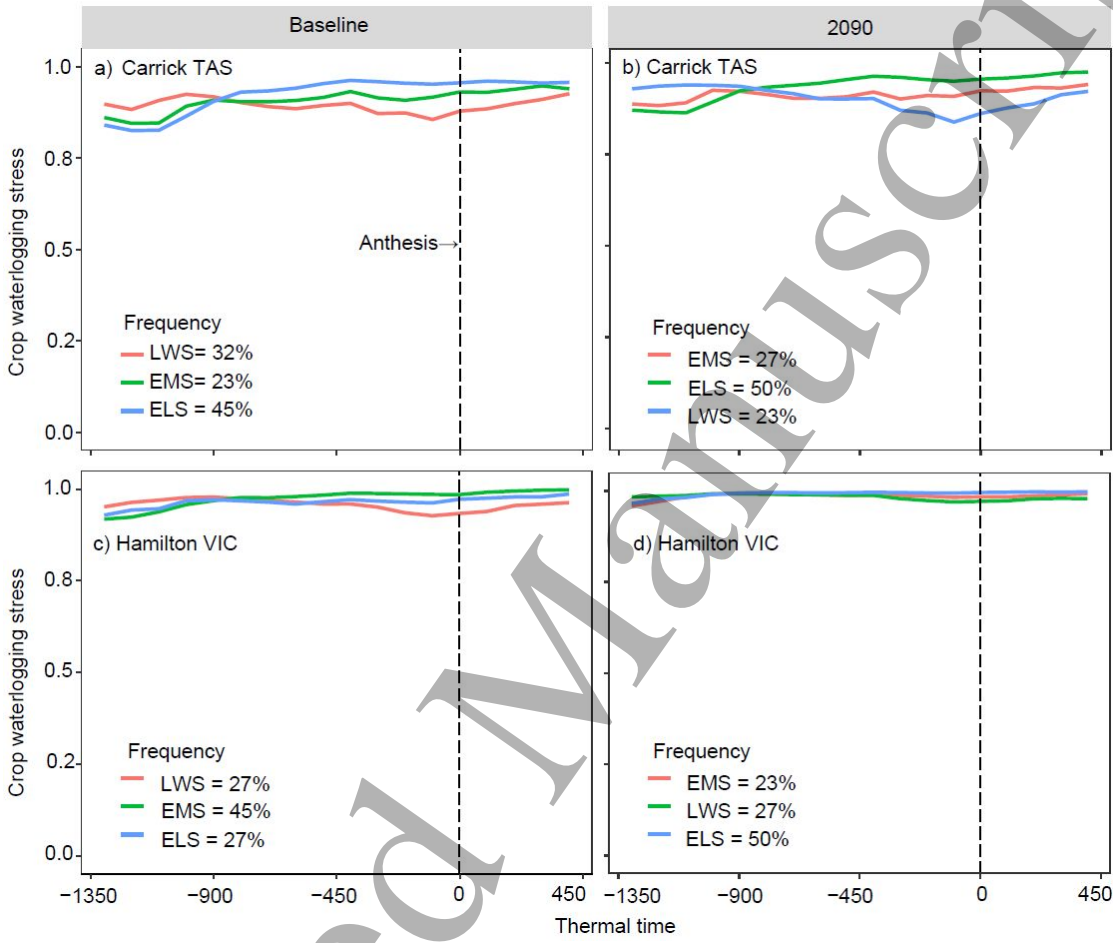


Fig. 6 Seasonal waterlogging stress clusters (1 = no stress, 0 = full stress) as a function of phenology centred on anthesis at Carrick, Tasmania (a, b) and Hamilton, Victoria (c, d). Left and right columns represent current and future climates, respectively (other sites are shown in the supplementary information). ELS: early-onset low waterlogging stress; EMS: early-onset medium waterlogging stress; LWS: late waterlogging stress.

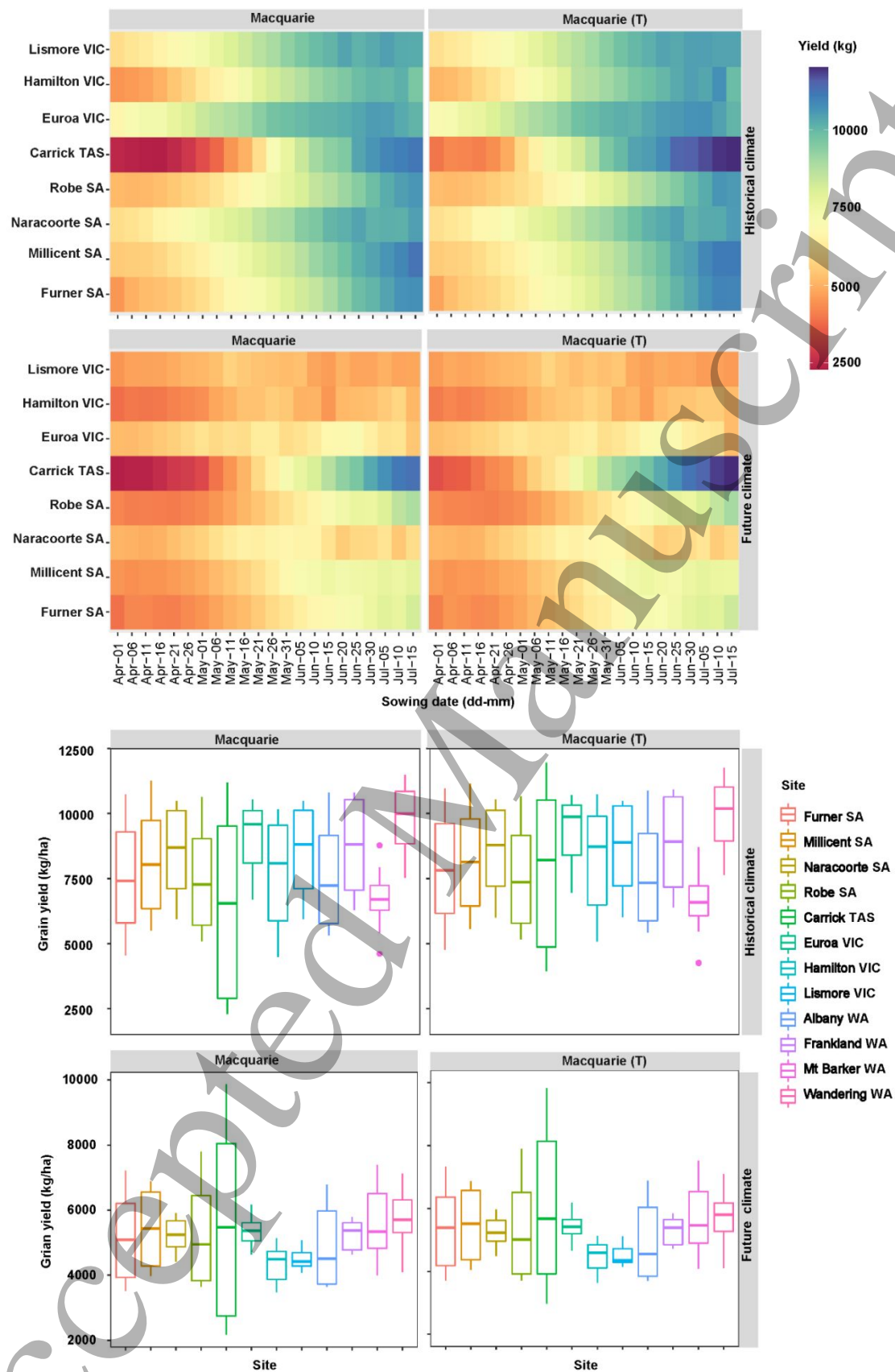


Fig. 7 Upper panel: Heatmap of simulated yield variation between waterlogging tolerant (Macquarie (T)) and susceptible (Macquarie) genotypes as a function of

sowing date under historical and future climates across sites. Waterlogging stress was relative minor in Western Australian, so this region was excluded. Values shown are averaged across years in which growing season rainfall is higher than the 90th percentile value. Lower panel: boxplots of simulated yield for waterlogging tolerant (Macquarie (T)) and susceptible (Macquarie) genotypes under historical and future climates.

4 Discussion

A central purpose of this study was to improve the capacity of APSIM-Barley to model the effects of waterlogging on barley growth and development through addition of processes affecting photosynthesis and phenology. We integrated new algorithms from APSIM-Soybean into APSIM-Barley with respect to the impacts of waterlogging on phenology and photosynthesis. We first showed that the ability of the default version of APSIM to simulate waterlogging was poor, because the model failed to adequately account for the effects of waterlogging on growth and phenology (Fig. 2). After addition and parameterisation of new relationships between waterlogging and photosynthesis and phenology, the validated model showed good correlation between simulated and observed phenology, maturity biomass, grain number and grain yield across genotypes and waterlogging treatments (Fig. S3&3). This work has built on the work of Pasley *et al* (2020) by using experimental greenhouse results to implement differential waterlogging stress impacts according to vegetative and reproductive phases of barley. We advanced their waterlogging algorithm by enabling different effects of waterlogging with phenology as suggested by our experimental data (Liu *et al* 2020a). It is also worth noting here that Pasley *et al* (2020) modelled the effects of waterlogging on a dicotyledon (soybean) whereas we modelled the effects of waterlogging on a monocotyledon (barley).

While effects of growth stress due to waterlogging early in the crop life cycle were well simulated, our results show a need to further improve the ability of APSIM to simulate waterlogging that occurs in later phenology. The relatively poor result for late waterlogging in waterlogging treatment 4 (Fig. S3&3) may be because grain number in APSIM-Barley is calculated as the product of stem dry matter on the last day of floral initiation with a cultivar-specific parameter that determines the number

of grains per stem (*grains_per_gram_stem*). Grain number in APSIM-Barley thus remains constant from last day of floral initiation. In unstressed conditions this assumption works well, but under waterlogged conditions, this assumption breaks down. Waterlogging stress just prior to or after heading reduces grain number, sometimes causing death of entire ears due to effects on spikelet fertility and grain filling (Liu *et al* 2020a). The overestimation of simulated grain number under late waterlogging shown here exemplifies this process. While our work is a significant step forwards in process-based modelling of waterlogging, this observation highlights an avenue for future improvement of the model.

Given such limitations in simulating late-stage waterlogging, is it perhaps serendipitous that waterlogging of autumn-sown cereal crops in Australia generally occurs during vegetative stages in winter (Fig. 6(a)&(b)). Our results suggest that waterlogging stresses should be included in future crop models, particularly in studies that cross-examine the capacity of crop models for scaling, inter- and ensemble model comparison efforts of climate change and greenhouse gas emissions (Farina *et al* 2021; Harrison *et al* 2016c), because waterlogging stress has and will have significant effects on simulated yield at some sites.

Although earlier flowering dates are expected under future climates in Australia (Gourdji *et al* 2013), few studies examine how OFPs across diverse environments will change under future climates. A notable exception is the study by Chen *et al* (2020), who found that OFPs of wheat will move forward by an average 29 days in the dry scenario and 11 days in the wet scenario under RCP 8.5 during 2061-2100 in Western Australia. These findings are consistent with our simulated results at sites in WA (e.g. Albany, Frankland and Mt Barker) but not at Wandering (30 days earlier). This is because relative temperature changes at Wandering are higher than other sites (Fig. S1) that are closer to the coast and experience more Mediterranean environments, thus advancing crop thermal time at a much higher rate.

Grain yields and OFPs in high rainfall environments are generally higher and wider, respectively, compared with environments that experience greater drought stress (Chen *et al* 2020; Liu *et al* 2019). Narrow OFPs in drought-prone environments

are due to higher risk of late spring frost, and/or earlier risk of heat or water-deficit stress. Late-spring frosts are more likely to occur in drought-prone regions due to clear sky nights, coupled with high pressure systems (DPIRD 2021). Cereals such as barley and wheat are most susceptible to frost damage around flowering, with single frost events having the potential to damage stems and completely desiccate heads (Zheng *et al* 2015). In high rainfall environments, daily temperatures are generally lower, and when coupled with higher rainfall during crop reproductive stages, terminal water stress tends to be alleviated (Phelan *et al* 2018). Here, we observed that OFPs will become wide due to increasingly severe high temperature stress under future climates. Wide OFPs suggest a uniform low-yielding environment over a wide range of sowing dates, such that there is little variation in yield under many flowering dates (Fig. 5). This is evidenced by the substantial yield reduction due to increasingly severe high temperature stress (–35% average reduction across locations, genotypes and sowing dates, Fig. 7).

In addition, the relative importance of waterlogging stress in determining OFPs will become less under future climates, as most simulated sites will have minor waterlogging stress due to decreased rainfall. We extended the previous assessments of climate change impact on crop production by simulating the combined impacts of the occurrence of frost and heat stress event together with water stress (deficit and excess) during the reproductive stages (Chen *et al* 2020, Flohr *et al* 2017, Hunt *et al* 2019, Lilley *et al* 2019). Such method combined with our waterlogging algorithms can be applied into diverse environments (e.g. from too little water to too much water or high temperature to low temperature).

The significant decline in yields with climate change shown in Fig. 7 is consistent with results in other rainfed Mediterranean environments under high emission scenarios (Potgieter *et al* 2013, Yang *et al* 2019). Similar results were also observed by Van Gool and Vernon (2006), who reported that climate change in Western Australia may result in large reductions (>30%) in barley potential yield in the northern agricultural region (around Mullewa) by 2050 due to reduced rainfall and higher maximum temperatures. To adapt to climate change, others have suggested that early-sown long-season varieties can sustain or improve wheat yield for future climatic

conditions (Hunt *et al* 2019, Zheng *et al* 2012). Such effects were not observed in our study, although the early-sown long-season genotype Macquarie had higher yield compared with the relatively fast developing (short-season) genotype Planet in most sites (except Carrick in Tasmania, where fast maturity genotypes obtained higher yields under future climates; Table S1). Similar to the observations made by Harrison *et al* (2014) for maize crops under future climates in Europe, these results suggest that earlier flowering in early terminal water stress environments is likely to result in higher yields, because crops have flowered and set seed before the majority of terminal water stress is realised.

In this study, we selected sites with different soil physics and growing season rainfall to examine the extent to which these factors influence waterlogging in APSIM. Our results show that sites with the combination of low soil hydraulic conductivity, low watertables and high growing season rainfall would have higher frequencies of waterlogging, evidenced by the evidence that low yields at Carrick and Furner (Fig. 5). Sites with high soil hydraulic conductivity, deep watertables and high growing season rainfall (e.g. Albany, Frankland and Mt Barker) would have little waterlogging stress compared with other sites. Euroa, Wandering and Millicent have similar soil characteristics with the only difference being soil hydraulic conductivity (Euroa having the lowest hydraulic conductivity). However, even in years of low rainfall, waterlogging stress occurred at Euroa, although waterlogging stress at Wandering and Millicent was often minimal. These findings suggest that soil hydraulic conductivity may be a governing factor of soil waterlogging stress in our study. Tests of the sensitivity of these factors were out of scope of current paper but would be an ideal avenue for future research.

Our results show that Tasmania would have similar waterlogging stress under both historical and future climates (Fig. 6). These results have important implications for barley breeding in Tasmania, for they indicate that current typologies (temporal exposure to waterlogging at certain crop stages) will be similar to those experienced in future. To concurrently increase yield potential and respond to climate change, many studies recommend improving tolerance to waterlogging stress in crops through breeding programs (Lobell *et al* 2015). Breeding of crop genotypes with improved

tolerance to waterlogging stress appears to be an effective adaptation strategy to climate change. Indeed, we showed that the waterlogging tolerant genotype Macquarie(T) can mitigate up to 23% yield penalty caused by waterlogging under historical and future climates in Tasmania, suggesting further research and development of waterlogging tolerance genetics would be a worthwhile investment. These results suggest selection of elite barley germplasm for superior yield under present conditions using field trials should be an appropriate method for developing germplasm suitable for 2090 conditions in Tasmania.

As for any study, the present paper had some limitations. We adopted an atmospheric CO₂ concentration of 850 ppm, as this value was the median of an ensemble of global climate models (GCMs) at 2090. If the main objective of the present study had been on climate change impacts per se, another level of complexity that could be added to the study might have been to conduct a factorial simulation with a range of CO₂ values, spanning the uncertainty in GCMs projections at 2090. These simulations could also account for the uncertainty in projected temperature and rainfall under future climates. However, the main focus of our study was the relative variability in the impacts of waterlogging across sites and the ability of waterlogging tolerance genetics to alleviate waterlogging stress. As such, we believe the approach taken here is both sensible and appropriate.

5 Conclusions

Accounting for the waterlogging on photosynthesis and phenology in APSIM significantly improved the ability of the model to simulate growth and development in waterlogged environments. While biophysical effects of early-stage waterlogging were well simulated, our results suggest a need to further improve the ability of the model to simulate late season waterlogging. Our factorial G×E×M analysis showed that waterlogging stresses will diminish but this was not enough to prevent substantial yield reduction due to increasingly severe high temperature stress (–35% average reduction in yield) under future climates. Planting waterlogging tolerant genotypes mitigate yield penalty caused by waterlogging by up to 6% and 4% under historical and future climates across sites.

Data availability statement

The data that support the findings of this study are available upon reasonable request from the authors.

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